Ecological Indicators 102 (2019) 1–9

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Seasonal dynamics of fine root respiration in the degraded and successional primary Korean pine forests in the Lesser Khingan mountains of Northern China

Yanmei Fu[a], Fujuan Feng[a,*], Xiaoxu Fan[b], Yanbo Hu[a], Xiuyue Zhang[a]

[a] School of Life Sciences, Northeast Forestry University, Harbin 150040, China
[b] School of Life Sciences, Heilongjiang University, Harbin 150080, China

ARTICLE INFO

Keywords:
Degenerate succession
Fine root respiration
Live fine root biomass
Pinus koraiensis
Soil carbon sequestration
Soil temperature

ABSTRACT

The broad-leaved and Korean pine mixed forests in the Liangshui National Natural Reserve, China, are important components of boreal forests in areas that are sensitive to global climate change. Respiration rates of excised roots were measured using an oxygen electrode (Hansatech Oxy-Lab 2, UK) to examine the variation in and identify the controlling factors of fine root respiration (Rr) during the growing period (May–October) in 2016. The relationships between Rr and biotic/abiotic factors [e.g., soil temperature, live fine root biomass (LFRB), and the soil carbon index] were subsequently analyzed. The results showed that Rr was significantly higher in the secondary broad-leaved forest (SF) than that in the primary Korean pine forest (PK) ($p < 0.001$); whereas soil carbon sequestration showed the opposite trend ($p < 0.05$). Rr tended to exponentially increase with soil temperature ($p < 0.001$) in both forest types. The Q_{10} value of the PK was significantly higher than that of the SF ($p < 0.01$). Pearson correlation and regression analyses revealed that Rr was significantly linearly correlated with LFRB, total soil organic carbon, soil soluble organic carbon, and soil microbial biomass carbon ($p < 0.01$). Stepwise regression was used to further explain that LFRB and soil microbial biomass carbon were the major contributors to changes in Rr ($F = 53.97$, $p < 0.001$, $R^2 = 0.75$). The findings of the present study offer insights into the variability of the soil carbon sink function in the degraded and successional primary Korean pine forests.

1. Introduction

Forest ecosystems account for 73% of terrestrial vegetation ecosystems and constitute the largest carbon storage pool. Forest ecosystems, therefore, play a leading role in the global carbon cycle (Brunori et al., 2016), and soil respiration in forest ecosystems is important with regards to the global carbon cycle and changing climate. Soil respiration is, therefore, major topic in some key research projects. Root respiration is a major contributor; accounting for 40–70% of the total soil respiration in forest ecosystems (Hanson et al., 2000; Thierron and Laudelout, 1996). Root respiration is an important factor that affects the carbon storage dynamics or balance in forest ecosystems, and is key to solving the “missing carbon sink” mystery and predicting future climate changes (Strong et al., 2017). Fine roots, which are characterized by a short growing period and rapid turnover, are a significant component of root bioenergy (Wang et al., 2016). Due to their large biomass, fine roots contribute a large portion to the total root respiration compared with the other belowground portions of forests; and they are also a major source of carbon input to the soil (Brüggemann et al., 2011). Fine root respiration is influenced by environmental factors, such as soil temperature, moisture, and nutrient availability (Jia et al., 2013; O’Neill et al., 2003) and by biological factors, such as forest age, root diameter class, and tree species (Miyatani et al., 2017). Recently, more attention has been focused on how differences in the soil physical, chemical, and biological properties, in response to the differing vegetation characteristics and management practices, drive the dynamics of fine root respiration (Li et al., 2016; Schneider et al., 2017); however, related studies are scarce. Thus, investigations on the driving mechanisms of fine root respiration dynamics are required.

The broad-leaved and Korean pine mixed forests in the Liangshui National Natural Reserve, China, are important components of boreal forests in the area, and are sensitive to global climate change. Broad-leaved and Korean pine mixed forests play a crucial role in the regional carbon balance (Wang, 2006) and global warming may strongly influence soil carbon dynamics by altering forest structure and function (Antonarakis, 2014). However, in recent years, Korean pine forests

* Corresponding author.
E-mail address: ffj9018@sina.com (F. Feng).

https://doi.org/10.1016/j.ecolind.2019.02.029
Received 22 November 2017; Received in revised form 14 January 2019; Accepted 12 February 2019
Available online 16 February 2019
1470-160X/

have been severely destroyed and gradually replaced by a large area of secondary broad-leaved forests (SF). Secondary forests regenerate as part of a climax community after the destructive anthropogenic disturbances of the original forest vegetation, and can alter forest ecological functions (Chen and Li, 2003). Studies on related carbon budget issues caused by the degraded succession of Korean pine forests are limited (Shi et al., 2015).

The dominant tree species in the climax community at late stage of succession often profoundly transform and affect the soil (Breemen and Finzi, 1998). If the constructive species (*Pinus koraiensis*) finally disappeared because of the degradation and succession of the climax community, the soil habitat would greatly change. This change may induce a feedback impact on fine root respiration; an important indicator of the diversification of forest carbon sink function during degraded community succession. Therefore, we hypothesized that the fine root respiration rate (Rr) would vary greatly with the degradation and succession of primary Korean pine forests. The respiration rates of excised fine roots were measured throughout the growing season (May–October), soil temperature effects on fine root respiration were investigated, and the relationships between fine root respiration and the live fine root biomass (LFRB) and soil carbon indices were explored. Our main objective was to identify the potential factors that affect the variability of Rr in degraded and successional primary Korean pine forests.

2. Materials and methods

2.1. Study sites

This study was conducted in the Liangshui National Natural Reserve (47°12′57″N-128°52′17″E, 47°12′49″N-128°52′12″E), Dailing District of Yi Chun City in Heilong Jiang Province in northern China. This region is characterized by a continental monsoon climate that presents windy days and low precipitation during the spring. Because of its higher latitude, the study site has a mean annual temperature of −0.3 °C, and mean annual maximum and minimum temperatures of 7.5 °C and −6.6 °C, respectively. The study area has an annual typical precipitation period of 120–150 days, a mean annual rainfall of 676 mm, and a mean relative humidity of 78%. The snow period lasts for 130–180 days. The research area is among the most typical and complete distribution areas of broad-leaved Korean pine mixed forests and consists of both original forest facies that have never been harvested and secondary forest phases that occurred following clear cutting and burning; therefore, the research area represents various stages of forest succession and occurrence.

Site A, a primary Korean pine forest; and site B, a secondary broad-leaved forest, were selected as the study sites within the area (Fig. 1). Both sites were distributional primary Korean pine forests before the 1960 s, but site B was subjected to clearly cutting in 1957 (i.e., almost all the trees and shrubs in the forest were cleared) which formed a secondary bare land. After nearly 60 years of restoration succession, the secondary broad-leaved forests have now matured. The two sites were adjacent to each other and exhibited similar ecological conditions (such as elevation, aspect, and soil parent material) (Table 1).

To reduce the spatial heterogeneity between the two sites, we selected quadrats that had similar aspects, gradients, slopes, and microtopography. Three fixed quadrats of 30 × 30 m (within a distance of 20 m from each other) were established at each site. Three “S” curves at equal intervals of 10 m were drawn and sampling points were set at 1 m intervals along the curves; i.e., there were 10 sampling points for each curve and 30 sampling points in each quadrat.

2.2. Experimental design

2.2.1. Fine roots and soil sampling

Surface soil cores (inner diameter: 5 cm) were collected using a soil auger at each sampling point. A total of 90 soil cores were collected from each site and transported to the laboratory in sterilized plastic bags. Each soil sample was mixed thoroughly and then divided into two parts: one part was first sieved and then stored at −80 °C, and the other was air-dried. The sieved soil samples were passed through 2, 1, 0.5, and 0.25 mm mixed soil sieves, after which the fine roots (diameter ≤2 mm) were washed with running water until they were completely separated from the soil particles. Based on the shape, color, and elasticity of the fine roots as well as the difficulty of root bark and column separation, we identified the live and dead fine roots and excluded the grassroots. As stated above, ten samples were randomly collected for each “S” curve at each quadrat, after which plant litter and plant and animal debris were removed from the samples. Soil bulk density was analyzed at each site.

2.2.2. Fine root respiration

The soil freezing period in the study site continued from early November to mid-April. Respiration rates of excised roots were measured from late May to October in 2016 (Bahn et al., 2006; Chen et al., 2015). Studies have shown that respiration rates of excised roots can account for about 50%–80% of the total root respiration (Bekku et al., 2009; Stockfors and Linder, 1998). The method of mixed fine root respiration determination was used (Burton et al., 2002). The intact fine roots of the 90 soil cores were all extracted and the mixed fine roots of the dominant species were selected from each soil core, of which the diameters were basically equal. The dominant tree species in the primary Korean pine forest were *Pinus koraiensis*, *Fraxinus mandschurica*, *Tilia mandshurica*, *Tilia amurensis*, *Acer mono*, *Acer ukurunduense*, *Acer tegmentosum*. The dominant tree species in the secondary broad-leaved forests were *F. mandschurica*, *T. amurensis*, *Phellodendron amurense*, *A. mono*. In previous publications, the oxygen electrode method (Hansatech Oxy-Lab 2, UK) has commonly been used to measure respiration rates of roots in vitro (Bouma et al., 2010; Clark et al., 2010; Jia et al., 2010). Subsequently, the extracted roots were divided into three parts, with each part weighing 0.1 g. We used a double-sided knife to cut fine roots into 2 mm segments, and then put them into the reaction cup to initiate the experiments. The temperature of the reaction cup was maintained at the same temperature as that of the surface soil (at a depth of 0–10 cm) at the time of field sampling. The process (from sampling to determination) was completed within 2.5 h (Rewald et al., 2014). A total of 270 (90 × 3) fine root parts of a mixture of dominant species were measured in each site and the monthly fine root respiration rate of each site was represented by the mean value. The soil temperature was synchronously measured using an electronic thermometer and three repetitions were performed for this parameter in each site. Soil temperature measurements were conducted for no less than 2 min each.

2.2.3. Live fine root biomass (LFRB)

Live fine roots were isolated and then placed in an oven at 80 °C until they were dried to a constant weight. The LFRB was calculated as follows:

$$\text{LFRB}\ (\text{t}\cdot\text{hm}^{-2}) = \text{the average live fine root weight of each soil core (g)} \times 100/[\pi(5.0/2)^2] \quad (1)$$

2.2.4. Soil carbon index analyses

The fine root total carbon (FRTC) was analyzed using a Multi N/C 2100s system (Analytik Jena, Germany). The total soil organic carbon (SOC) was analyzed in accordance with the oxidized method using potassium dichromate (Li et al., 2017). The soil easily oxidized organic carbon (EOC) was measured in accordance with the potassium permanganate oxidation method using 333 mM $KMnO_4$ as an extractant (Dou et al., 2008). The concentrations of the SOC and EOC were both measured using a visible spectrophotometer (JH-14-08 723, China).

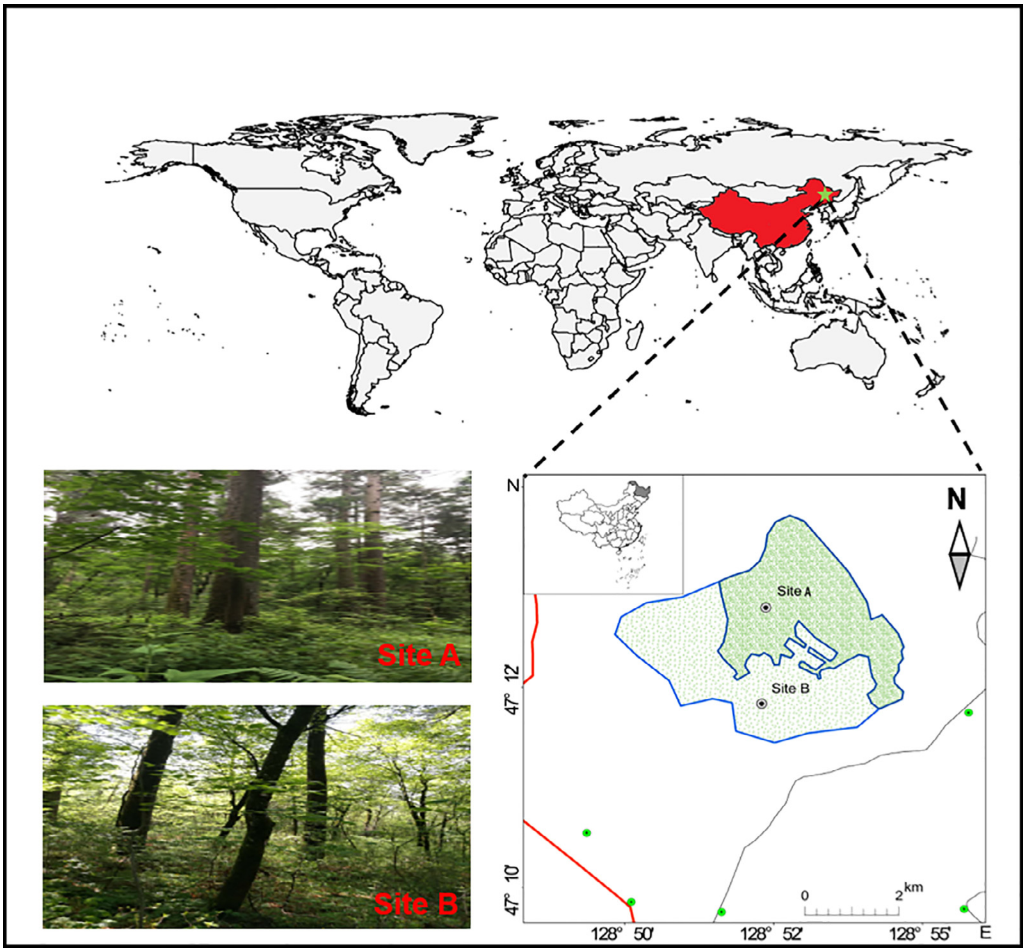

Fig. 1. Map of world and location of the two study sites in Liangshui National Natural Reserve in Heilongjiang Province, north of China. Site A, primary Korean pine forest (PK) and Site B, secondary broad-leaved forest (SF).

The soil dissolved organic carbon (DOC) and microbial biomass carbon (MBC) were both measured in accordance with the chloroform fumigation-extraction method using 0.5 M K_2SO_4 as an extractant (Jiang et al., 2006). The concentrations of DOC and MBC were both analyzed using a total organic carbon analyzer (Vario TOC Cube, Elementar, Germany).

2.2.5. Soil bulk density

The soil bulk density was measured using a soil cutting ring (100 cm^3) (Sandoval et al., 2013)

2.2.6. Soil C sequestration

Soil carbon value in PK and SF were calculated using the formula:

$$C = H \times \rho \times B \times 10 \quad (2)$$

where C is SOC reserve ($t{\cdot}hm^{-2}$), H soil thickness (m), ρ is soil bulk density ($g{\cdot}cm^{-3}$), B content of SOC ($g{\cdot}kg^{-1}$), and 10 is the conversion factor.

2.3. Statistical analyses

Before analysis of variance and testing of statistical significance, we first checked the normality of distribution (Kolmogorov-Smirnov test) and homogeneity (Levene's test) of all the variables. A one-way analysis of variance with a *t*-test was used to check the differences of Rr, temperature sensitivity coefficients of fine root respiration rate (Q_{10}), and the C sequestration between the two forest stands across the growing season, as well as the differences in the LFRB, FRTC, SOC, and labile soil organic carbon. Statistical significance was established at the 5% level. The relationship between seasonal Rr and soil temperature were examined using an exponential model. Correlation and regression analyses were used to determine the relationships of LFRB, FRTC, SOC, DOC, EOC, and MBC with Rr. Subsequently, we used a stepwise regression analysis to identify the main factors that affected fine root respiration. The significance of all regression equations was analyzed using the F-test at the 5% level. The analyses were conducted using SPSS 18.0 (SPSS Inc., Chicago, Illinois, USA) and R version 3.3.1 (R

Table 1
Overview of the two study areas of the Liangshui National Natural Reserve in Heilongjiang Province, north of China.

Forest type	Geographical position	Altitude (m)	Main tree species
PK	47°12′57″N 128°52′17″E	402	*Pinus koraiensis*, *Fraxinus mandschurica*, *Tilia mandshurica*, *Tilia amurensis*, *Acer mono*, *Acer ukurunduense*, *Acer tegmentosum*, *Ulmus laciniata*, *Syringa reticulata* var. *amurensis*, *Padus racemosa*, *Betula costata*
SF	47°12′49″N 128°52′12″E	390	*F. mandschurica*, *T. amurensis*, *Phellodendron amurense*, *A. mono*, *P. racemosa*, *S. reticulata* var. *amurensis*, *U. laciniata*

PK, primary Korean pine forest; SF, secondary broad-leaved forest.

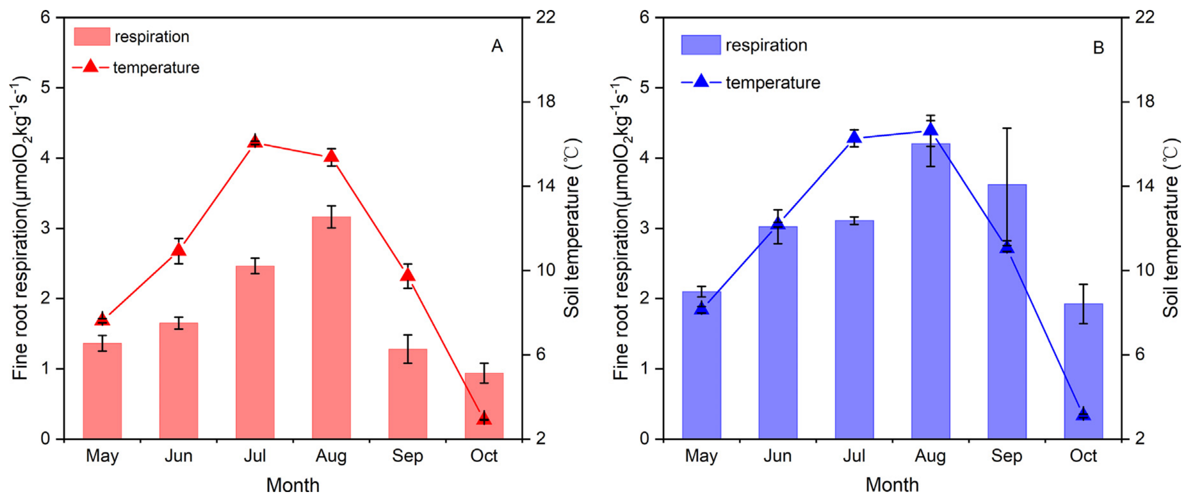

Fig. 2. Fine root respiration and soil temperature dynamics at 0–10 cm depth in the primary Korean pine forest (A) and secondary broad-leaved forest (B) during the growing season.

Core Team 2016). The index of the Rr response to temperature can also be described by the Q_{10} value, which is defined as the difference in respiration rate in response to a 10 °C change (Shi et al., 2016). The Q_{10} value was calculated using the exponential relationship between Rr and soil temperature (Zogg et al., 1996) as follows:

$$Rr = a \cdot exp^{bT} \quad (3)$$

where Rr is the fine root respiration ($\mu molO_2\, kg^{-1}\, s^{-1}$), T is the 0–10 cm soil temperature (°C) and a and b are constants fitted to the regression equation, and

$$Q_{10} = exp^{10b} \quad (4)$$

where b is a constant fitted to formula 3.

3. Results

3.1. Growth seasonal dynamics of fine root respiration and soil temperature

Rr for the two forest types followed a "single peak" curve and the variation in Rr was correlated with that of soil temperature (Fig. 2A, B). Rr increased gradually from May to August, and the peak values (3.16 $\mu molO_2\, kg^{-1}\, s^{-1}$ for the primary Korean pine forests (PK) and 4.35 $\mu molO_2\, kg^{-1}\, s^{-1}$ for the secondary broad-leaved forests (SF)) were observed in August. Rr values for both the PK and SF decreased with decreasing temperature and reached a minimum in October. Rr in the PK ranged from 0.94 to 3.16 $\mu molO_2 kg^{-1} s^{-1}$ (average: 1.81 $\mu molO_2\, kg^{-1}\, s^{-1}$). The Rr values in the SF ranged from 1.92 to 4.35 $\mu molO_2\, kg^{-1}\, s^{-1}$ (average: 3.02 $\mu molO_2\, kg^{-1}\, s^{-1}$). The fine root respiration rate of SF was significantly higher (1.67-fold over the entire growing season, $p < 0.001$) than that of PK (Fig. 3).

3.2. Growth seasonal variations in LFRB/soil carbon index and SOC sequestration

During the growing season, the general effects of the forest type on LFRB and the soil carbon index are depicted in Fig. 4. The mean LFRB of the secondary broad-leaved forests (SF) was significantly greater than that of the primary Korean pine forests (PK) ($F = 76.78$, $p < 0.01$); the average LFRB of SF was 19.40% greater than that of PK (Table 2). The mean total SOC ($F = 8.01$, $p < 0.05$), the soil EOC ($F = 42.60$, $p < 0.01$) and soil MBC ($F = 86.14$, $p < 0.01$) of SF were all significantly greater than that of PK throughout the growing season; the mean FRTC ($F = 1.90$, $p > 0.05$) and soil DOC ($F = 7.46$, $p > 0.05$) did not significantly differ during this time (Table 2).

In addition, the soil C sequestration was assessed (Lai et al., 2016; Sun et al., 2013) by calculating the difference between the final and initial SOC storage in the 0–10 cm soil layer (Eq. (2)). The soil carbon sink value was 32.89 $t{\cdot}hm^{-2}$ and 27.22 $t{\cdot}hm^{-2}$ in the PK and SF, respectively (Table 3), and the values were significant different ($F = 8.55$, $p < 0.05$).

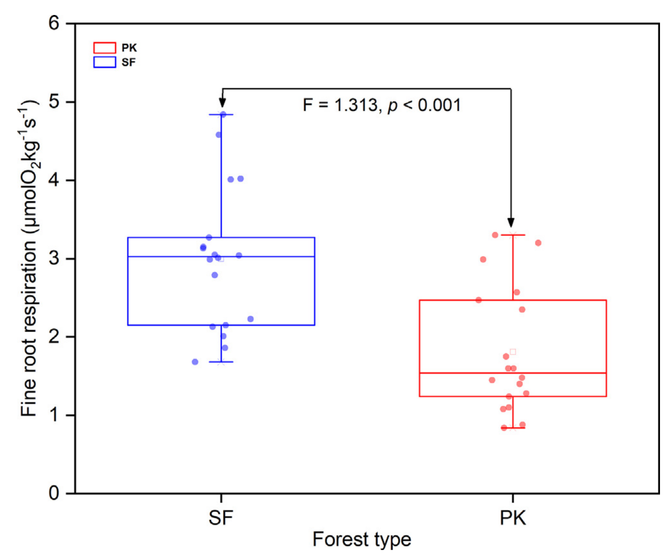

Fig. 3. Fine root respiration of the primary Korean pine forest (PK) and secondary broad-leaved forest (SF). The boxes represent the range of the first and third quartiles; the horizontal lines in the boxes represent the median; The dots in the boxes denote fine root respiration. Significant differences between the forest types were identified using a *t*-test ($p < 0.001$).

3.3. Relationship of soil temperature with fine root respiration

Using the Eq. (3), the fine root respiration rate (Rr) and soil temperature of two forest types were fitted by regression. During the study period, Rr showed an exponential, positive relationship with soil temperature with $R^2 = 0.87$ ($p < 0.001$) and $R^2 = 0.66$ ($p < 0.001$) in the PK and SF, respectively (Fig. 5A, B). Temperature sensitivity (Q_{10}) was estimated to be 2.38 ± 0.24 and 1.70 ± 0.06 in the PK and SF, respectively (Eq. (4)). The Q_{10} value in PK was significantly greater than that in SF ($F = 22.09$, $p < 0.01$).

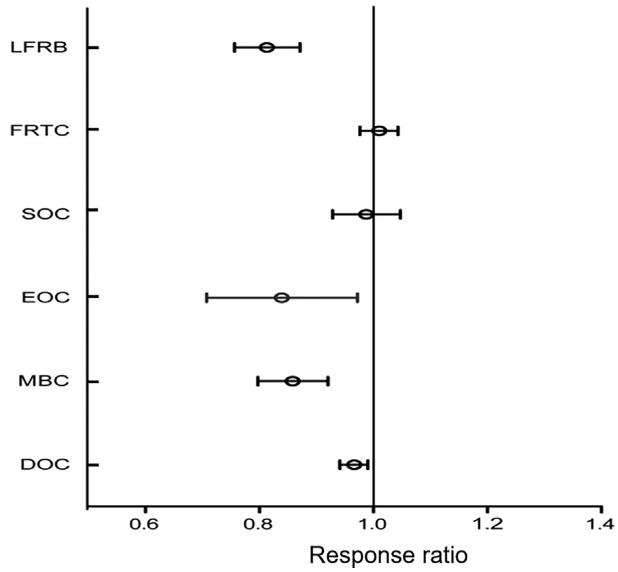

Fig. 4. Mean response ratios for the LFRB/soil carbon index calculated in the growing season between the primary Korean pine forest (PK) and secondary broad-leaved forest (SF). Live fine root biomass (LFRB), fine root total carbon (FRTC), total soil organic carbon (SOC), soil easily oxidized organic carbon (EOC), microbial biomass carbon (MBC), and soil dissolved organic carbon (DOC).

3.4. Relationships between the fine root respiration and LFRB/soil carbon index

Pearson correlation coefficient by psych packages in R revealed the degree of correlation between Rr and the selected environmental factors (Fig. 6). During the growing season, Rr significantly increased linearly with increasing the LFRB, SOC, DOC, and MBC ($p < 0.01$) (Fig. 7 A, C, E, F). However, no strong linear correlations were observed between FRTC / EOC and Rr ($p > 0.05$) (Fig. 7 B, D). Stepwise regression further revealed that LFRB and soil MBC were the major contributors to changes in Rr (Table 4) and that LFRB and MBC collectively explained 75% of the variation observed in the fine root respiration rate.

4. Discussion

4.1. Diversification of fine root respiration and the soil carbon sequestration after the degradation of primary Korean pine forests

Rr of the PK was significantly lower than that of the SF ($p < 0.001$), and the average Rr of the SF was 1.67 times that of the PK during growing season (from May to October) (Fig. 3). From early November to mid-April of the following year, the soil of the region froze, the fine roots became dormant, and respiration ceased (Enzai and Jingyun, 2014; Li et al., 2018). The measured results were, therefore, representative of the annual and seasonal variation in fine root respiration. Root respiration is an important part of the underground carbon cycle (Sun et al., 2017). A significant increase in root respiration accelerates the loss of carbon from underground pools and leads to increased soil CO_2 emissions to the atmosphere (Harrison et al., 1993). As shown in Table 3, the soil carbon sink values of the PK and SF were 32.89 $t{\cdot}hm^{-2}$ and 27.22 $t{\cdot}hm^{-2}$, respectively, and were significantly different ($p < 0.05$). Compared to the primary Korean pine forests, the carbon sink capacity of the secondary broad-leaved forests was 21% lower. Throughout the entire growing season, the fine root respiration was significantly higher in the primary Korean pine forests that had degenerated into the secondary broad-leaved forests, which thus resulted in the increased outflow of nutrients and carbon from the soil.

Table 2
Monthly variations in live fine root biomass (LFRB), fine root total carbon (FRTC), soil organic carbon (SOC), and labile SOC pools: soil dissolved organic carbon (DOC), microbial biomass carbon (MBC), and soil easily oxidized organic carbon (EOC) of two forest types. Data represent means ± SDs.

Forest type	Primary Korean pine (PK)						Secondary broad-leaved (SF)					
Month	LFRB	FRTC	SOC	Labile SOC pools			LFRB	FRTC	SOC	Labile SOC pools		
	($t{\cdot}hm^{-2}$)	($mg{\cdot}g^{-1}$)	($g{\cdot}kg^{-1}$)	DOC ($mg{\cdot}kg^{-1}$)	MBC ($mg{\cdot}kg^{-1}$)	EOC ($g{\cdot}kg^{-1}$)	($t{\cdot}hm^{-2}$)	($mg{\cdot}g^{-1}$)	($g{\cdot}kg^{-1}$)	DOC ($mg{\cdot}kg^{-1}$)	MBC ($mg{\cdot}kg^{-1}$)	EOC ($g{\cdot}kg^{-1}$)
May	2.24 ± 0.07	460.13 ± 5.22	70.20 ± 1.54	417.96 ± 6.95	537.80 ± 16.40	12.92 ± 1.01	2.82 ± 0.19	445.60 ± 7.78	65.76 ± 0.97	426.60 ± 14.42	638.26 ± 6.42	24.72 ± 1.78
June	2.54 ± 0.11	488.78 ± 3.28	66.19 ± 1.44	453.88 ± 5.51	854.13 ± 22.69	12.64 ± 0.39	3.24 ± 0.27	476.19 ± 7.34	72.20 ± 1.22	481.94 ± 10.96	1081.49 ± 97.44	13.97 ± 2.03
July	2.71 ± 0.06	450.56 ± 1.17	73.97 ± 1.07	506.80 ± 9.04	933.00 ± 13.08	11.49 ± 0.67	2.90 ± 0.07	461.26 ± 2.70	76.02 ± 4.93	543.13 ± 13.79	873.68 ± 6.26	22.98 ± 1.74
August	2.85 ± 0.07	440.24 ± 0.95	82.59 ± 4.47	559.40 ± 10.03	1077.33 ± 78.50	12.58 ± 0.52	3.56 ± 0.17	493.07 ± 4.00	98.85 ± 1.85	581.48 ± 9.78	1168.73 ± 57.80	11.89 ± 0.94
September	2.03 ± 0.06	480.91 ± 2.80	65.05 ± 4.14	575.66 ± 3.85	951.00 ± 47.28	21.12 ± 1.41	3.01 ± 0.02	464.87 ± 8.93	66.44 ± 1.86	588.43 ± 10.21	1200.94 ± 10.56	23.95 ± 4.06
October	1.58 ± 0.37	495.51 ± 13.82	66.58 ± 4.10	459.62 ± 58.35	567.73 ± 35.28	24.12 ± 1.91	1.79 ± 0.01	453.36 ± 11.54	58.09 ± 2.80	460.01 ± 10.84	782.10 ± 50.01	21.38 ± 1.53
Mean	2.33 ± 0.47	469.36 ± 22.28	70.76 ± 6.65	495.55 ± 57.25	820.17 ± 219.36	15.81 ± 5.38	2.89 ± 0.60	465.73 ± 17.16	72.91 ± 14.15	513.60 ± 61.27	957.53 ± 227.58	19.81 ± 5.49

Table 3
Soil C sequestration [soil organic C (SOC)] at 0–10 cm soil depth in the primary Korean pine forest (PK) and secondary broad-leaved forest (SF) between May and October 2016.

Forest type	Soil ρ ($g·cm^{-3}$)	SOC content ($g·kg^{-1}$)	SOC stock ($t·hm^{-2}$)	SOC sequestration ($t·hm^{-2}$)
PK	1.52 ± 0.02 1.11 ± 0.02	70.20 ± 1.54 66.58 ± 4.10	106.73 ± 3.01 73.84 ± 4.17	32.89 ± 2.80a
SF	1.35 ± 0.01 1.06 ± 0.04	65.76 ± 0.97 58.09 ± 2.80	88.88 ± 1.80 61.66 ± 3.58	27.22 ± 1.85b

Different letters indicate significant differences between PK and SF ($p < 0.05$).

This may explain the decline in the soil carbon sink throughout the growing season after the degraded succession of primary Korean pine forests (Lee et al., 2005). In fact, aboveground vegetation and litter input are another two important sources of SOC (Proietti et al., 2016; Xiong et al., 2018). The carbon sequestration capacity of Matiwane forests and secondary forests were compared in South Africa and the results showed that the carbon sequestration capacity of the secondary forests had decreased by approximately 25% (Mangwale et al., 2017). After the primary Korean pine forests degenerated into the secondary broad-leaved forests, stand structure became relatively simple; aboveground biomass and average annual litter both decreased (Bowden et al., 1993; Mu et al., 2013). These changes could affect the amount of nutrients returned to the spoil and thus result in the reduction of the soil carbon sink (Kavvadias et al., 2001). Therefore, the protection of the primary Korean pine forests and promotion of the succession of the secondary broad-leaved forests to the climax community (*P. koraiensis*) are of great importance to improve the carbon sink capacity and ecological restoration of the forest ecosystem. In the present study, we observed significant differences in soil carbon sequestration between the PK and SF. However, these differences reflected the results of only one growing season. More accurate conclusions could be drawn from long-term observations.

4.2. Fine root respiration sensitivity to soil temperature after degraded succession in primary Korean pine forest

In the present study, the soil temperature and Rr showed similar trends throughout the whole growing season (Fig. 2), and soil temperature significantly positively impacted Rr ($p < 0.001$) (Fig. 5A, B). Soil temperature affects fine root respiration (Jia et al., 2011), and an exponential, positive correlation relationship exists between these factors. Q_{10} values are usually used to indicate the sensitivity of fine root respiration to soil temperature (Chen et al., 2009). The Q_{10} values of the PK and SF were 2.38 and 1.70, respectively, and were within the general range of variation (1.5–3.0) for fine root respiration (Ryan

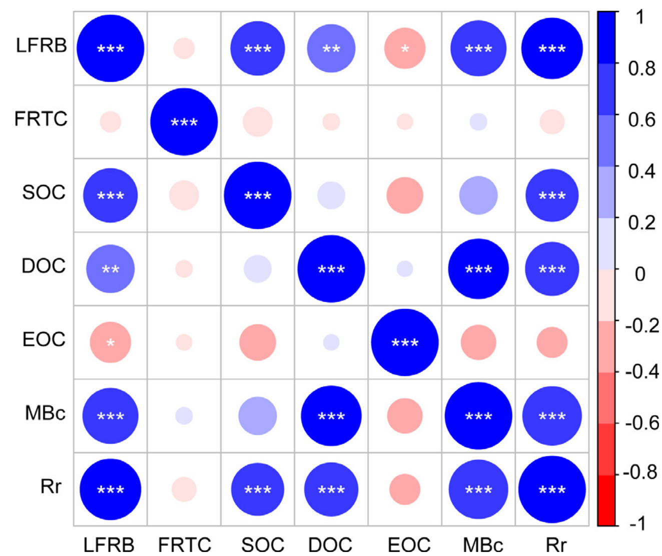

Fig. 6. Pearson's correlation coefficients between soil chemical properties [live fine root biomass (LFRB), fine root total carbon (FRTC), total soil organic carbon (SOC), soil dissolved organic carbon (DOC), soil easily oxidized organic carbon (EOC), and microbial biomass carbon (MBC)] and fine root respiration (Rr). Circles represent the correlation coefficients. The larger the circle, the higher the correlation coefficient. *, **, and *** represent significant differences at $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively.

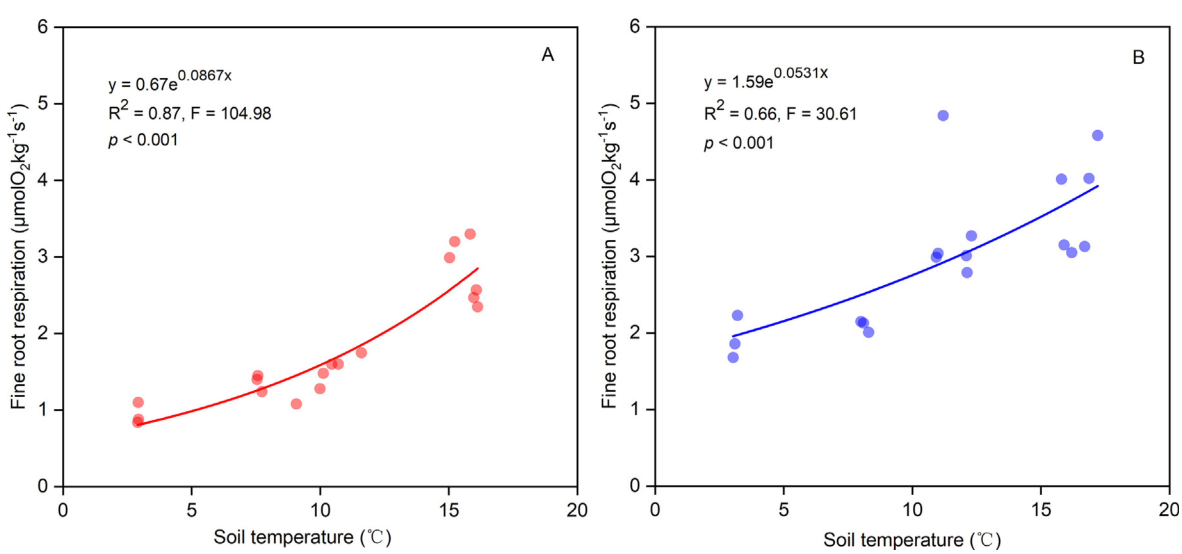

Fig. 5. The relationship between fine root respiration and soil temperature in the primary Korean pine forest (A) and secondary broad-leaved forest (B). Regression equations are highly significant ($p < 0.001$).

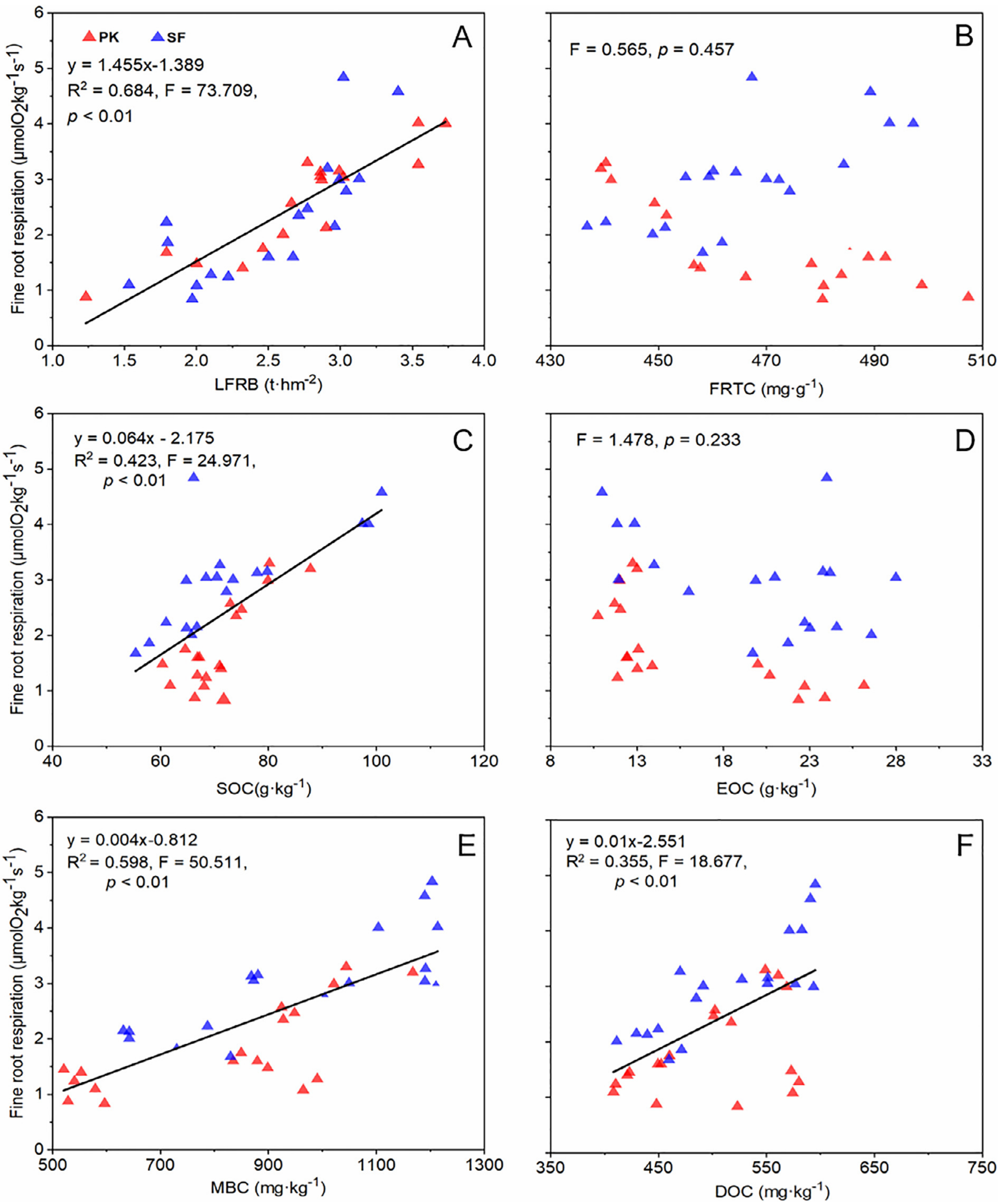

Fig.7. Relationships between the fine root respiration and the other parameters: live fine root biomass (LFRB, A), fine root total carbon (FRTC, B), total soil organic carbon (SOC, C), soil easily oxidized organic carbon (EOC, D), microbial biomass carbon (MBC, E), and soil dissolved organic carbon (DOC, F) in the primary Korean pine forest (PK) and secondary broad-leaved forest (SF).

et al., 1996). The Q_{10} value of the PK was significantly greater than that of the SF ($p < 0.01$), which indicated that fine root respiration in the PK was more sensitive to soil temperature variations. The temperature sensitivity of the Rr generally decreases after the degraded succession of virgin forests. For example, Guo et al. (2010) reported Q_{10} values that showed a decreasing trend following clear cutting. Yan et al. (2009) also reported Q_{10} values that significantly decreased following the degradation of evergreen broad-leaved forests and succession into secondary *Pinus massoniana* forests. The Q_{10} value of root respiration is substrate dependent (Ruehr and Buchmann, 2010). Substrate supply capacity varies with soil temperature; therefore, the substrate supply can influence the temperature sensitivity of root respiration (Yuste et al., 2010). The PK had a more diverse community composition than the SF, and had more developed root systems (Chen et al., 2003) which require more photosynthetic products for use as substrates for fine root respiration (Bauhus et al., 1998), which therefore may explain the higher temperature sensitivity of the fine roots in the PK than those in the SF. Global surface temperatures are predicted to increase by

Table 4
Results of a stepwise regression between soil properties [live fine root biomass (LFRB) and microbial biomass carbon (MBC)] and fine root respiration.

Model	Coefficient	Normalization coefficient	R^2	F	Adjusted R^2	VIF
Constant	−1.793		0.766	53.970	0.752	
LFRB	0.986	0.561**				1.870
MBC	0.002	0.390**				1.870

** Indicates significance at $p < 0.01$.

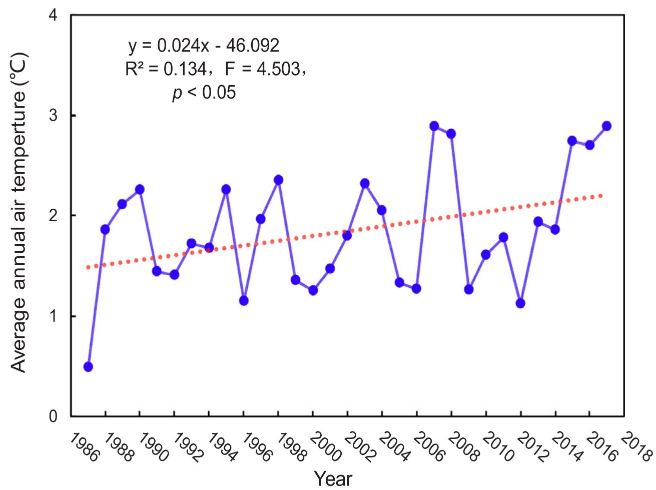

Fig. 8. Variations in the average annual air temperatures in the Liangshui National Natural Reserve in Northeastern China.

1.5–2.0 °C by the end of this century (Lotstein, 2013), and the average temperatures in this specific study region have increased by 0.2 °C every ten years (Fig. 8). Therefore, the future warming of the climate is expected to increase the release of CO_2 from soil through fine root respiration, and the findings of the present study indicate that such effects may tend to be higher in the primary Korean pine forests.

4.3. *The relationships between fine root respiration and LFRB and the soil carbon index*

The results indicated that the soil fertility indexes changed significantly ($p < 0.05$) (Fig. 4 and Table 2) after the degradation of the primary Korean pine forests. Fine root respiration exhibits great temporal and spatial variability and is controlled by many factors (Shi and Jin, 2016). Primary productivity and net primary productivity have been shown to change significantly after the degradation of a forest ecosystem, and such changes can lead to variations in biomass accumulation, which further influences root respiration by impacting soil fertility (Jiang et al., 2005; Vesterdal et al., 2012). Lai et al. (2016) also reported that root respiration in forests was strongly dependent on photosynthesis and soil nutrient content. It is still unknown whether changes in these factors affect fine root respiration. Rr was significantly positively correlated with LFRB ($p < 0.01$). The LFRB significantly increased after the degraded succession of PK, which led to increased carbohydrate proportions of the substrate (Yan et al., 2015) and thereby increased Rr. The LFRB can be considered as a major indicator of fine root respiration intensity and it plays an important role in predicting the amount of CO_2 released via fine root respiration (Gong et al., 2012). In addition, Rr was also significantly positively correlated with the soil carbon indicators (SOC, DOC, and MBC) ($p < 0.01$) (Fig. 7). These indicators represent soil nutrient availability (Huang et al., 2017), and significant alterations to these indicators can lead to changes in the water and nutrient absorption capacity of fine roots (Bowden et al., 1993; King et al., 2010); therefore, variations in these indicators can cause changes in fine root respiration. The stepwise regression analysis revealed that the LFRB and MBC collectively explained 75% of the variation (Table 4). The findings indicated that increases in the LFRB and soil MBC content were closely related to the significant rise in fine root respiration rate after the degraded succession of primary Korean pine forests.

5. Conclusions

The present study showed that degraded succession of the primary Korean pine forests led to a significant increase in Rr and a reduction in soil C sequestration in the growing season. The exponential model showed that Rr was sensitive to soil temperature changes, i.e., the Q_{10} value in PK was higher than that in SF. Moreover, both LFRB and soil MBC were more closely related to the variation in respiration rate of fine roots in the degraded and successional primary Korean pine forests. These findings provide an accurate scientific basis for the quantification of the mechanisms that drive fine root respiration in degraded and successional primary Korean pine forests.

Conflicts of interest

The authors declare there are no conflicts of interest.

Acknowledgments

This work was financially supported by the National Natural Science Foundation of China (approved: 31670496) and the Fundamental Research Funds for the Central Universities (approved: 2572015EA02).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.02.029. These data include Google maps of the most important areas described in this article.

References

Antonarakis, A.S., 2014. Uncertainty in initial forest structure and composition when predicting carbon dynamics in a temperate forest. Ecol. Model. 291, 134–141. https://doi.org/10.1016/j.ecolmodel.2014.07.030.

Bahn, M., Knapp, M., Garajova, Z., Pfahringer, N., Cernusca, A., 2006. Root respiration in temperate mountain grasslands differing in land use. Glob. Chang. Biol. 12, 995–1006. https://doi.org/10.1111/j.1365-2486.2006.01144.x.

Bauhus, J., Paré, D., Coté, L., 1998. Effects of tree species, stand age and soil type on soil microbial biomass and its activity in a southern boreal forest. Soil Biol. Biochem. 30, 1077–1089. https://doi.org/10.1016/s0038-0717(97)00213-7.

Bekku, Y.S., Sakata, T., Nakano, T., Koizumi, H., 2009. Midday depression in root respiration of *Quercus crispula* and *Chamaecyparis obtusa*: its implication for estimating carbon cycling in forest ecosystems. Ecol. Res. 24, 865–871. https://doi.org/10.1007/s11284-008-0560-7.

Bouma, T.J., Yanai, R.D., Elkin, A.D., Hartmond, U., Floresalva, D.E., Eissenstat, D.M., 2010. Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. New Phytol. 150, 685–695. https://doi.org/10.1046/j.1469-8137.2001.00128.x.

Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Melillo, J.M., Garrison, J.B., 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res. 23, 1402–1407. https://doi.org/10.1139/x93-177.

Breemen, N. Van, Finzi, A.C., 1998. Plant-soil interactions: ecological aspects and evolutionary implications. Biogeochemistry 42, 1–19. https://doi.org/10.1007/978-94-017-2691-7_1.

Brüggemann, N., Gessler, A., Kayler, Z., Keel, S.G., Badeck, F., Barthel, M., Boeckx, P., Buchmann, N., Brugnoli, E., Esperschütz, J., 2011. Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: a review. Biogeosciences 8, 3619–3695. https://doi.org/10.5194/bgd-8-3619-2011.

Brunori, A., Sdringola, P., Dini, F., Ilarioni, L., Nasini, L., Regni, L., Proietti, P., Proietti, S., Vitone, A., Pelleri, F., 2016. Carbon balance and life cycle assessment in an oak plantation for mined area reclamation. J. Clean. Prod. 144, 69–78. https://doi.org/10.1016/j.jclepro.2016.12.116.

Burton, A.J., Pregitzer, K.S., Ruess, R.W., Hendrik, R.L., Allen, M.F., 2002. Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. Oecologia 131, 559–568. https://doi.org/10.1007/s00442-002-0931-7.

Chen, D., Wang, Y., Lan, Z., Li, J., Xing, W., Hu, S., Bai, Y., 2015. Biotic community shifts explain the contrasting responses of microbial and root respiration to experimental soil acidification. Soil Biol. Biochem. 90, 139–147. https://doi.org/10.1016/j.soilbio.2015.08.009.

Chen, D., Yang, Z., Lin, Y., Hua, C., Fu, S., 2009. Stand level estimation of root respiration for two subtropical plantations based on in situ measurement of specific root respiration. For. Ecol. Manage. 257, 2088–2097. https://doi.org/10.1016/j.foreco.2009.02.018.

Chen, X., Li, B.L., 2003. Change in soil carbon and nutrient storage after human disturbance of a primary Korean pine forest in Northeast China. For. Ecol. Manage. 186, 197–206. https://doi.org/10.1016/s0378-1127(03)00258-5.

Chen, X., Li, B.L., Lin, Z.S., 2003. The acceleration of succession for the restoration of the mixed-broadleaved Korean pine forests in Northeast China. For. Ecol. Manage. 177, 503–514. https://doi.org/10.1016/s0378-1127(02)00455-3.

Clark, N.M., Apple, M.E., Nowak, R.S., 2010. The effects of elevated CO_2 on root respiration rates of two Mojave Desert shrubs. Glob. Chang. Biol. 16, 1566–1575. https://doi.org/10.1111/j.1365-2486.2009.02075.x.

Dou, F., Wright, A.L., Hons, F.M., 2008. Sensitivity of labile soil organic carbon to tillage in wheat-based cropping systems. Soil Sci. Soc. Am. J. 72, 1445–1453. https://doi.org/10.2136/sssaj2007.0230.

Enzai, D., Jingyun, F., 2014. Linking belowground and aboveground phenology in two boreal forests in Northeast China. Oecologia 176, 883–892. https://doi.org/10.1007/s00442-014-3055-y.

Gong, J., Ge, Z., An, R., Duan, Q., You, X., Huang, Y., 2012. Soil respiration in poplar plantations in northern China at different forest ages. Plant Soil 360, 109–122. https://doi.org/10.1007/s11104-011-1121-3.

Guo, J.F., Yang, Y.S., Chen, G.S., Xie, J.S., Ren, G., Wen, Q., 2010. Effects of clear-cutting and slash burning on soil respiration in Chinese fir and evergreen broadleaved forests in mid-subtropical China. Plant Soil 333, 249–261. https://doi.org/10.1007/s11104-010-0339-9.

Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48, 115–146. https://doi.org/10.1023/a:1006244819642.

Harrison, K., Broecker, W., Bonani, G., 1993. A strategy for estimating the impact of CO_2 fertilization on soil carbon storage. Global Biogeochem. Cycles 7, 69–80. https://doi.org/10.1029/92gb02938.

Huang, W., Liu, J., Han, T., Zhang, D., Huang, S., Zhou, G., 2017. Different plant covers change soil respiration and its sources in subtropics. Biol. Fertil. Soils 53, 469–478. https://doi.org/10.1007/s00374-017-1186-0.

Jia, S., Mclaughlin, N.B., Gu, J., Li, X., Wang, Z., 2013. Relationships between root respiration rate and root morphology, chemistry and anatomy in *Larix gmelinii* and *Fraxinus mandshurica*. Tree Physiol. 33, 579–589. https://doi.org/10.1093/treephys/tpt040.

Jia, S., Wang, Z., Li, X., Sun, Y., Zhang, X., Liang, A., 2010. N fertilization affects on soil respiration, microbial biomass and root respiration in *Larix gmelinii* and *Fraxinus mandshurica* plantations in China. Plant Soil 333, 325–336. https://doi.org/10.1007/s11104-010-0348-8.

Jia, S., Wang, Z., Li, X., Zhang, X., Mclaughlin, N.B., 2011. Effect of nitrogen fertilizer, root branch order and temperature on respiration and tissue N concentration of fine roots in *Larix gmelinii* and *Fraxinus mandshurica*. Tree Physiol. 31, 718–726. https://doi.org/10.1093/treephys/tpr057.

Jiang, L., Shi, F., Li, B., Luo, Y., Chen, J., Chen, J., 2005. Separating rhizosphere respiration from total soil respiration in two larch plantations in northeastern China. Tree Physiol. 25, 1187–1195. https://doi.org/10.1093/treephys/25.9.1187.

Jiang, P.K., Xu, Q.F., Xu, Z.H., Cao, Z.H., 2006. Seasonal changes in soil labile organic carbon pools within a *Phyllostachys praecox* stand under high rate fertilization and winter mulch in subtropical China. For. Ecol. Manage. 236, 30–36. https://doi.org/10.1016/j.foreco.2006.06.010.

Kavvadias, V.A., Alifragis, D., Tsiontsis, A., Brofas, G., Stamatelos, G., 2001. Litterfall, litter accumulation and litter decomposition rates in four forest ecosystems in northern Greece. For. Ecol. Manage. 144, 113–127. https://doi.org/10.1016/s0378-1127(00)00365-0.

King, J.S., Albaugh, T.J., Allen, H.L., Buford, M., Strain, B.R., Dougherty, P., 2010. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol. 154, 389–398. https://doi.org/10.1046/j.1469-8137.2002.00393.x.

Lai, Z., Lu, S., Zhang, Y., Wu, B., Qin, S., Feng, W., Liu, J., Fa, K., 2016. Diel patterns of fine root respiration in a dryland shrub, measured in situ over different phenological stages. J. For. Res. 21, 31–42. https://doi.org/10.1007/s10310-015-0511-4.

Lee, M.S., Nakane, K., Nakatsubo, T., Koizumi, H., 2005. The importance of root respiration in annual soil carbon fluxes in a cool-temperate deciduous forest. Agric. For. Meteorol. 134, 95–101. https://doi.org/10.1016/j.agrformet.2005.08.011.

Li, X., Guo, D., Zhang, C., Niu, D., Fu, H., Wan, C., 2018. Contribution of root respiration to total soil respiration in a semi-arid grassland on the Loess Plateau, China. Sci. Total Environ. 627, 1209–1217. https://doi.org/10.1016/j.scitotenv.2018.01.313.

Li, Y., Hou, C., Song, C., Guo, Y., 2016. Seasonal changes in the contribution of root respiration to total soil respiration in a freshwater marsh in Sanjiang Plain, Northeast China. Environ. Earth Sci. 75, 848. https://doi.org/10.1007/s12665-016-5592-7.

Li, Z., Liu, C., Dong, Y., Chang, X., Nie, X., Liu, L., Xiao, H., Lu, Y., Zeng, G., 2017. Response of soil organic carbon and nitrogen stocks to soil erosion and land use types in the Loess hilly–gully region of China. Soil Tillage Res. 166, 1–9. https://doi.org/10.1016/j.still.2016.10.004.

Lotstein, E.L., 2013. Global climate change impacts in the United States: a state of knowledge report from the U.S. Global Climate Change Research Program. J. Environ. Qual. 40, 279. https://doi.org/10.2134/jeq2010.0010br.

Mangwale, K., Shackleton, C.M., Sigwela, A., 2017. Changes in forest cover and carbon stocks of the coastal scarp forests of the Wild Coast, South Africa. South. For. J. For. Sci. 79, 1–11. https://doi.org/10.2989/20702620.2016.1255480.

Miyatani, K., Tanikawa, T., Makita, N., Hirano, Y., 2017. Relationships between specific root length and respiration rate of fine roots across stands and seasons in *Chamaecyparis obtusa*. Plant Soil 423, 215–227. https://doi.org/10.1007/s11104-017-3499-z.

Mu, C., Lu, H., Wang, B., Bao, X., Cui, W., 2013. Short-term effects of harvesting on carbon storage of boreal *Larix gmelinii – Carex schmidti*i forested wetlands in Daxing'anling, northeast China. For. Ecol. Manage. 293, 140–148. https://doi.org/10.1016/j.foreco.2012.12.031.

O'Neill, K.P., Kasischke, E.S., Richter, D.D., 2003. Seasonal and decadal patterns of soil carbon uptake and emission along an age sequence of burned black spruce stands in interior Alaska. J. Geophys. Res. Atmos. 108, 11–15. https://doi.org/10.1029/2001JD000443. FFR 11-1-FFR.

Proietti, P., Sdringola, P., Brunori, A., Ilarioni, L., Nasini, L., Regni, L., Pelleri, F., Desideri, U., Proietti, S., 2016. Assessment of carbon balance in intensive and extensive tree cultivation systems for oak, olive, poplar and walnut plantation. J. Clean. Prod. 112, 2613–2624. https://doi.org/10.1016/j.jclepro.2015.10.009.

Rewald, B., Rechenmacher, A., Godbold, D.L., 2014. Focus issue on roots: it's complicated: intraroot system variability of respiration and morphological traits in four deciduous tree species. Plant Physiol. 166, 736–745. https://doi.org/10.1104/pp.114.240267.

Ruehr, N.K., Buchmann, N., 2010. Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities differ among microbial and root-rhizosphere respiration. Tree Physiol. 30, 165. https://doi.org/10.1093/treephys/tpp106.

Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J., Mcmurtrie, R.E., 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol. 16, 333. https://doi.org/10.1093/treephys/16.3.333.

Sandoval, M., Celis, J., Pedreros, L., Capulín, J., 2013. Chemical remediation of an agricultural soil: a case study of the tsunami-affected area of Chile. Water Air Soil Pollut. 224, 1–10. https://doi.org/10.1007/s11270-013-1590-5.

Schneider, H.M., Wojciechowski, T., Postma, J.A., Brown, K.M., Lücke, A., Zeisler, V., Schreiber, L., Lynch, J.P., 2017. Root cortical senescence decreases root respiration, nutrient content and radial water and nutrient transport in barley. Plant Cell Environ. 40, 1392–1408. https://doi.org/10.1111/pce.12933.

Shi, B., Gao, W., Cai, H., Jin, G., 2016. Spatial variation of soil respiration is linked to the forest structure and soil parameters in an old-growth mixed broadleaved-Korean pine forest in northeastern China. Plant Soil 400, 1–12. https://doi.org/10.1007/s11104-015-2730-z.

Shi, B., Gao, W., Jin, G., 2015. Effects on rhizospheric and heterotrophic respiration of conversion from primary forest to secondary forest and plantations in northeast China. Eur. J. Soil Biol. 66, 11–18. https://doi.org/10.1016/j.ejsobi.2014.11.003.

Shi, B., Jin, G., 2016. Variability of soil respiration at different spatial scales in temperate forests. Biol. Fertil. Soils 52, 561–571. https://doi.org/10.1007/s00374-016-1100-1.

Stockfors, J., Linder, S., 1998. Effect of nitrogen on the seasonal course of growth and maintenance respiration in stems of Norway spruce trees. Tree Physiol. 18, 155–166. https://doi.org/10.1093/treephys/18.3.155.

Strong, A.L., Johnson, T.P., Chiariello, N.R., Field, C.B., 2017. Experimental fire increases soil carbon dioxide efflux in a grassland long-term multifactor global change experiment. Glob. Chang. Biol. 23, 1975–1987. https://doi.org/10.1111/gcb.13525.

Sun, B.W., Yang, X.D., Zhang, Z.H., Wen-Ji, M.A., Ali, A., Huang, H.X., Yan, E.R., 2013. Relationships between soil carbon pool and vegetation carbon return through succession of evergreen broad-leaved forests in Tiantong region, Zhejiang Province, Eastern China. Chin. J. Plant Ecol. 37, 803–810. https://doi.org/10.3724/sp.j.1258.2013.00084.

Sun, L., Ataka, M., Kominami, Y., Yoshimura, K., 2017. Relationship between fine-root exudation and respiration of two Quercus species in a Japanese temperate forest. Tree Physiol. 37, 1–10. https://doi.org/10.1093/treephys/tpx026.

Thierron, V., Laudelout, H., 1996. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. Can. J. For. Res. 26, 1142–1148. https://doi.org/10.1139/x26-127.

Vesterdal, L., Bo, E., Christiansen, J.R., Callesen, I., Schmidt, I.K., 2012. Soil respiration and rates of soil carbon turnover differ among six common European tree species. For. Ecol. Manage. 264, 185–196. https://doi.org/10.1016/j.foreco.2011.10.009.

Wang, C., 2006. Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. For. Ecol. Manage. 222, 9–16. https://doi.org/10.1016/j.foreco.2005.10.074.

Wang, C., Han, S., Zhou, Y., Zhang, J., Zheng, X., Dai, G., Li, M.H., 2016. Fine root growth and contribution to soil carbon in a mixed mature *Pinus koraiensis* forest. Plant Soil 400, 275–284. https://doi.org/10.1007/s11104-015-2724-x.

Xiong, Y., Liao, B., Proffitt, E., Guan, W., Sun, Y., Wang, F., Liu, X., 2018. Soil carbon storage in mangroves is primarily controlled by soil properties: a study at Dongzhai Bay, China. Sci. Total Environ. 619–620, 1226–1235. https://doi.org/10.1016/j.scitotenv.2017.11.187.

Yan, J., Zhang, D., Zhou, G., Liu, J., 2009. Soil respiration associated with forest succession in subtropical forests in Dinghushan Biosphere Reserve. Soil Biol. Biochem. 41, 991–999. https://doi.org/10.1016/j.soilbio.2008.12.018.

Yan, M., Guo, N., Ren, H., Zhang, X., Zhou, G., 2015. Autotrophic and heterotrophic respiration of a poplar plantation chronosequence in northwest China. For. Ecol. Manage. 337, 119–125. https://doi.org/10.1016/j.foreco.2014.11.009.

Yuste, J.C., Janssens, I.A., Carrara, A., Ceulemans, R., 2010. Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. Glob. Chang. Biol. 10, 161–169. https://doi.org/10.1111/j.1529-8817.2003.00727.x.

Zogg, G.P., Zak, D.R., Burton, A.J., Pregitzer, K.S., 1996. Fine root respiration in northern hardwood forests in relation to temperature and nitrogen availability. Tree Physiol. 16, 719–725. https://doi.org/10.1093/treephys/16.8.719.